Testing ecological release as a compensating mechanism for mass mortality in a keystone predator

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ABSTRACT: Top predator decline has been ubiquitous across systems over the past decades and centuries, and predicting changes in resultant community dynamics is a major challenge for ecologists and managers. Ecological release predicts that loss of a limiting factor, such as a dominant competitor or predator, can release a species from control, thus allowing increases in its size, density, and/or distribution. The 2014 sea star wasting syndrome (SSWS) outbreak decimated populations of the keystone predator *Pisaster ochraceus* along the Oregon coast, USA. This event provided an opportunity to test the predictions of ecological release across a broad spatial scale and determine the role of competitive dynamics in top predator recovery. We hypothesized that after *P. ochraceus* loss, populations of the subordinate sea star *Leptasterias* sp. would grow larger, more abundant, and move downshore. We based these predictions on prior research in Washington State showing that *Leptasterias* sp. competed with *P. ochraceus* for food. Further, we predicted that ecological release of *Leptasterias* sp. could provide a bottleneck to *P. ochraceus* recovery. Using field surveys, we found no clear change in density or distribution in *Leptasterias* sp. populations post-SSWS, and decreases in body size. In a field experiment, we found no evidence of competition between similar-sized *Leptasterias* sp. and *P. ochraceus*. Thus, the mechanisms underlying our predictions were not in effect along the Oregon coast, which we attribute to differences in habitat overlap and food availability between the 2 regions. Our results suggest that response to the loss of a dominant competitor can be unpredictable even when based in theory and previous research.

KEY WORDS: Compensation · Competition · Ecological release · Keystone predation · Mass mortality · Oregon · Rocky intertidal · Sea star wasting

1. INTRODUCTION

Characterizing the role of species interactions in determining community structure remains a fundamental pursuit in ecology. Many examples exist in terrestrial and marine systems illustrating the structuring role of top predators. Seminal work by Paine (1966, 1969) introduced the concept of a 'keystone' predator to describe a species that, through trophic interactions, plays a disproportionately large role in determining community structure relative to its abundance. In Paine's experiment, removal of the predatory sea star *Pisaster ochraceus* on Tatoosh Island, Washington, USA, resulted in drastic shifts in prey populations.

Specifically, California mussels *Mytilus californianus*, the dominant space occupier in the mid-intertidal zone, were able to move lower and crowd out the diverse species that occupy the low intertidal zone. This transformative work inspired decades of research attempting to identify and predict where keystone predation occurs, with respect to both keystone species identity and environmental context (Power et al. 1996, Menge & Sanford 2013, Menge et al. 2013).

Mass mortality of top predators, particularly when they play a keystone role in community organization, can lead to significant changes in community structure and functioning. In some contexts, however, abiotic and biotic factors at a specific site may mediate

the effects of top predator loss and prevent large shifts in community structure. For example, one prediction of 'ecological release' maintains that, in the event of a disappearance or decrease in density of one species, another species may be released from control (arising from processes such as competition with or predation from the first species) (Kohn 1978, Bolnick et al. 2010). In response, this species may expand in density, distribution, or behavior. Such changes can have cascading, often unanticipated, effects on other species in the ecosystem. For example, management measures taken in Florida to control raccoon predation on sea turtle eggs had the unintended effect of releasing ghost crab mesopredators from control by raccoons and resulted in increased turtle egg predation (Barton & Roth 2008).

In 2013 and 2014, sea star wasting syndrome (SSWS) devastated populations of most intertidal and subtidal sea star species along the entire North American west coast, including *P. ochraceus* (Hewson et al. 2014, Menge et al. 2016, Miner et al. 2018, Moritsch & Raimondi 2018). SSWS has been called the most extensive disease outbreak ever documented in a marine species (Eisenlord et al. 2016; whether this was truly a 'disease' remains under debate; Hewson et al. 2018, 2019), and has already led to shifts in community structure in some places (Schultz et al. 2016, Burt et al. 2018). In Oregon, *P. ochraceus* populations declined drastically over the course of summer 2014 in density (59 to 84% across the sites studied) and biomass (60 to 90%) (Menge et al. 2016). However, an unprecedented surge of recruits along much of the Oregon coast (i.e. 7–300 times more recruits in 2015 as opposed to 2014) led to an increase in *P. ochraceus* density in 2015 at all but one site surveyed (Menge et al. 2016).

Oregon populations of *Leptasterias* sp., a small 6-armed sea star, were less affected by SSWS than *P. ochraceus* and many other species (B. A. Menge & J. Sullivan-Stack unpubl. data). In the 1960s, the role of *Leptasterias* sp. in the intertidal community was investigated in the San Juan Islands, WA, USA (Menge 1972a,b, 1975, Menge & Menge 1974). That work showed that (1) the diets of *P. ochraceus* and *Leptasterias* sp. were similar; (2) adults of the 2 species competed, with the much larger *P. ochraceus* being a dominant interference competitor over *Leptasterias* sp.; (3) the size ranges of recruits (<10 g wet weight) and small juveniles (10–20 g wet weight) of *P. ochraceus* and adult *Leptasterias* sp. were similar; (4) *Leptasterias* sp. were far more abundant than were juvenile *P. ochraceus*; and (5) *Leptasterias* sp. adults were dominant exploitation competitors over

P. ochraceus juveniles (Menge 1972b, Menge & Menge 1974). These results suggested the hypothesis that exploitation competition with *Leptasterias* sp. created a bottleneck by limiting survival of *P. ochraceus* recruits. However, this interaction remained unstudied in more wave-exposed coasts such as those in Oregon, where *Leptasterias* sp. are smaller but prey are more available (B. A. Menge & J. Sullivan-Stack unpubl. data). The diet of *Leptasterias* sp. is broader than that of adult *P. ochraceus* (Menge 1972b, Menge & Menge 1974), but *P. ochraceus* diets are more varied at the recruit stage (Menge & Menge 1974, Sewell & Watson 1993). *Leptasterias* sp. and recruit *P. ochraceus* diets are similar in Oregon: *Leptasterias* sp. consume acorn barnacles (36% of feeding observations), small gooseneck barnacles (33%), limpets (14%), small mussel recruits (14%), and isopods (3%), all of which are typically <1 cm in length or diameter. In comparison, *P. ochraceus* recruits consume small acorn barnacles (43% of feeding observations), small gooseneck barnacles (35%), limpets (3%), small mussels (7%), small herbivorous snails (4%), whelks (3%), and polychaetes (4%) (B. A. Menge & J. Sullivan-Stack unpubl. data). Thus, if competition for resources between adult *Leptasterias* sp. and juvenile *P. ochraceus* occurs along the wave-exposed Oregon coast, as hypothesized for the San Juan Islands, populations of *Leptasterias* sp. could provide a barrier to *P. ochraceus* population recovery after SSWS. This would be particularly important if *Leptasterias* sp. populations respond to SSWS-driven loss of *P. ochraceus* in a manner consistent with ecological release.

The SSWS context provided a unique opportunity for testing whether inferences from small-scale experimental studies, such as sea star removal from one intertidal bench in Paine's seminal keystone experiment, scale up to natural conditions affecting populations along the entire west coast of the USA. Here, we asked (1) how did *Leptasterias* sp. populations respond to the SSWS-driven loss of *P. ochraceus* adult density; (2) what is the role of interactions with *Leptasterias* sp. in modulating the potential for *P. ochraceus* recovery from SSWS; and (3) how do these responses vary at different sites along the Oregon coast? We hypothesized that interspecific competition with *Leptasterias* sp. would limit *P. ochraceus* juvenile survival and therefore provide a bottleneck for population recovery. Specifically, we predicted that, in response to *P. ochraceus* biomass declines, *Leptasterias* sp. populations would follow the expectations of ecological release, by increasing in individual size and population density and changing habitat

preferences to occupy portions of the intertidal previously dominated by *P. ochraceus*, and thereby would limit growth of *P. ochraceus* recruits, inhibiting or slowing population recovery.

2. MATERIALS AND METHODS

2.1. Study system

We conducted surveys at 4 sites along the Oregon coast, USA: Strawberry Hill (SH; 44.250° N, 124.115° W) and Yachats Beach (YB; 44.319° N, 124.109° W) on Cape Perpetua, and Fogarty Creek (FC; 44.837° N, 124.0587° W) and Boiler Bay (BB; 44.832° N, 124.061° W) on Cape Foulweather (Fig. 1). Invertebrate prey productivity is relatively higher at Cape Perpetua than at Cape Foulweather (Menge et al. 2015). Prior to the SSWS outbreak in 2014, *Pisaster ochraceus* densities were 8.8 times higher at Cape Perpetua sites than at Cape Foulweather sites (means ± SE, 1.32 ± 0.1 versus 0.15 ± 0.02 ind. 0.25 m^{-2}, respectively), while *Leptasterias* sp. densities were only 1.5 times greater at Cape Perpetua sites (0.75 ± 0.1 versus 0.51 ± 0.07 ind. 0.25 m^{-2}; n = 571 and 548 quadrats sampled, respectively, in 2006–2012).
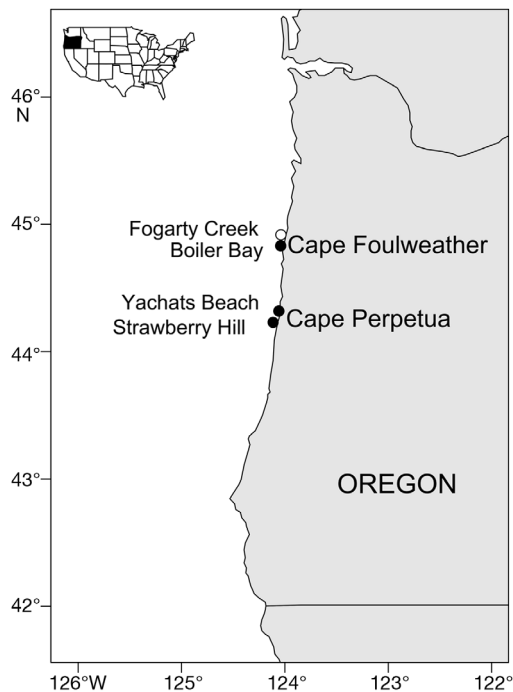

Fig. 1. Map of study sites along the Oregon coast, USA. The white point at Fogarty Creek indicates where we carried out the competition experiment in addition to surveys, and black points indicate survey sites

2.2. Size and density surveys

The size range of *P. ochraceus* is enormous, from 0.01 g in newly settled individuals to >1000 g, while the size of *Leptasterias* sp. ranges to 10 g maximum wet weight on the Oregon coast versus ≥20 g wet weight in the San Juan Islands (Menge 1972b, J. Sullivan-Stack & B. A. Menge unpubl. data). The broadcast spawner *P. ochraceus* reaches reproductive maturity at 70–100 g (Menge 1975, B. A. Menge, unpubl. data), while the brooding *Leptasterias* sp. matures at 2 g. Based on these data and estimates of the size reached by young-of-the-year *P. ochraceus* by their first summer (maximum of 10 g, most reach ~5 g), we use the term 'recruits' to refer to *P. ochraceus* that are less than 10 g, and juveniles as individuals 10–70 g in wet weight. Thus, *Leptasterias* sp. and *P. ochraceus* recruits are of similar size.

To assess changes in the size distribution and density of *Leptasterias* sp. populations in response to SSWS, we measured and counted sea stars in 0.25 m^2 quadrats along horizontal transects at all sites in the spring and summer of 2014, 2015, and 2017. To focus on the area of greatest spatial overlap of *P. ochraceus* recruits and *Leptasterias* sp., quadrats overlapped the lower edge of the mussel bed and the upper edge of the low zone; this habitat placement was consistent across years. Within each quadrat, we quantified sea star number and individual arm lengths (from the center of body to the tip of the longest arm). In 2014 and 2017, we surveyed 3 quadrats that were placed at 1, 3, and 5 m along 5 transects. In 2015, 5 adjacent quadrats were surveyed along 5 replicate 2.5 m transects. Although these methods were slightly different across years, the area of intertidal surveyed and type of data obtained were consistent, so we believe size and density comparisons across years are valid. In addition, strong wave action sometimes precluded finishing all transects, particularly in spring 2014. The number of transects sampled per site/year were as follows — BB: 2 (2014), 5 (2015), 5 (2017); FC: 2 (2014), 5 (2015), 5 (2017); SH: 2 (2014), 5 (2015), 5 (2017); and YB: 4 (2014), 3 (2015), 5 (2017). Thus, size and density survey data are uneven in time and space; as detailed below, we accounted for this unevenness in our analyses.

2.3. Habitat use

We predicted that in response to reduced abundance of adult *P. ochraceus*, habitat use of *Leptasterias* sp. populations would differ in 2017 compared to

2014. Specifically, we expected that *Leptasterias* sp. would shift their distribution lower on the shore to take advantage of newly available prey resources. Thus, we conducted habitat surveys for *Leptasterias* sp. and *P. ochraceus* coincidentally with size and density surveys at our sites during the spring (April–May) and summer (July) of 2014 and 2017, noting the location of each sea star as either within or outside of the mussel bed.

2.4. Vertical distribution surveys

To assess the prediction that loss of *P. ochraceus* adults from SSWS would result in *Leptasterias* sp. expanding their distribution downshore, we surveyed the vertical distribution of *Leptasterias* sp. and *P. ochraceus*. Surveys were conducted at the 4 sites in July 2014 (immediately post-SSWS), July 2015, and July 2017 (3 yr after peak SSWS). Sampling was conducted in mid-summer each year to minimize seasonally driven distribution changes. We used permanently marked (with stainless steel lag screws at the top and bottom) vertical transects (n = 5) to quantify sea star density in 0.25 m² quadrats within each of 5 intertidal zones (listed from low to high): low intertidal zone upper edge (dominated by algae and barnacles), mussel bed lower edge, mussel bed middle, mussel bed upper edge, and high zone.

2.5. Competition experiment

In 2015, we conducted field experiments to test the hypothesis that *Leptasterias* sp. adults compete for food with *P. ochraceus* recruits. Experiments used enclosures consisting of 5 cm high × 10 cm wide PVC or ABS plastic cylinders with a 2.5 cm wide stainless

steel ring on the bottom edge (Sioux Chief Total Knockout Debris Cover/Test Cap toilet flanges, product 886-4ATMPK) (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m637p059_supp.pdf). To facilitate water flow, we drilled 2 rows of holes spaced 2.5 cm (1 inch) apart around the sides and 7 holes in the bottom of the enclosures. To keep sea stars from escaping through the holes, we lined the inside with plastic mesh (window screening) secured with super glue followed by hot glue. The top was a circle of plastic mesh secured with a stainless-steel tightening ring (Fig. S1). Enclosures were fastened using three 0.467 cm (3/16 inch) lag screws inserted through holes in the stainless steel ring and screwed into plastic wall anchors placed in predrilled holes in the rock. We used this new enclosure design instead of the standard stainless steel mesh cages widely used in intertidal experiments (e.g. Connell 1961, Dayton 1971, Menge 1976, Menge et al. 2003, 2016) because in pilot experiments, the small size and dexterity of the sea stars allowed them to escape from cages of traditional design.

Enclosures were set up in the ecological low zone of the intertidal zone (just below the *Mytilus californianus* mussel bed) at FC, with each treatment replicated 5 times (Fig. S1). Treatments included (1) 4 *Leptasterias* sp. individuals, no *P. ochraceus* (*Leptasterias* sp. low density; LL); (2) 4 *P. ochraceus*, no *Leptasterias* sp. (*P. ochraceus* low density; PL); (3) 4 *Leptasterias* sp. and 4 *P. ochraceus* (mixed high density; MH); (4) 8 *Leptasterias* sp., no *P. ochraceus* (*Leptasterias* sp. high density; LH); and (5) 8 *P. ochraceus*, no *Leptasterias* sp. (*P. ochraceus* high density; PH) (Table 1). In each treatment of 5 replicates at each site, we quantified growth, survival, and behavior of both species over the 3-mo course of the experiment.

If *Leptasterias* sp. are indeed better food competitors, we predicted that *P. ochraceus* in the MH treat-

Table 1. Details of treatments for sea star enclosure field experiment

Treatment	No. *Leptasterias* sp.	No. *P. ochraceus*	Comparisons
Leptasterias sp. low density (LL)	4	0	Establish baseline growth; compare with LH to test intraspecific competition
Leptasterias sp. high density (LH)	8	0	Compare with MH to test interspecific competition; compare with LL to test intraspecific competition
P. ochraceus low density (PL)	0	4	Establish baseline growth; compare with PH to test intraspecific competition
P. ochraceus high density (PH)	0	8	Compare with MH to test interspecific competition; compare with PL to test intraspecific competition
Mixed high density (MH)	4	4	Compare with PL and PH to test interspecific competition

ment would grow slower than those in either of the other *P. ochraceus* treatments (PL or PH). Alternatively, if *P. ochraceus* recruits were not affected by species identity but only by total sea star density relative to prey, we would expect each species of sea star in the low-density treatments (LL and PL) to exhibit higher growth than that same species in the high-density treatments (MH, LH and PH). Direct comparison between *Leptasterias* sp. and *P. ochraceus* growth is not biologically meaningful, as these sea stars were at different life stages (*Leptasterias* sp. adults and *P. ochraceus* recruits) and are unlikely to have the same energy allocation to growth versus reproduction and maintenance.

Before assigning sea stars to treatments, we measured the wet weight (after blotting with a paper towel) and sea star arm length (from the center of the body to the tip of the longest arm) of each sea star to the nearest 0.001 g and 0.01 mm, respectively. Starting weights were not significantly different across sea star species (Welch 2-sample *t*-test, $t = -1.29$, df = 160, p = 0.20; mean ± SE starting weight for *Leptasterias* sp. = 0.42 ± 0.04 g, *P. ochraceus* = 0.51 ± 0.05 g; Fig. S2). Sea stars were assigned randomly to treatment, and enclosures were deployed 17 July 2015.

Mytilus trossulus was used as prey for this experiment due to the fact that it is present in both *Leptasterias* sp. and *P. ochraceus* recruit diets, it is common, it is sessile and thus cannot easily escape the predators, and can be manipulated without damage. We added 4 *M. trossulus* mussels, each between 10 and 20 mm length, to the center of each enclosure. We chose to use 4 mussels to ensure prey availability was limiting and to promote competition. At each monthly sampling, we measured empty mussel shells and added the appropriate number of mussels to reach a total of 4. We also noted what part of the enclosure the sea star was in (bottom, side, or top) and whether it was hiding under mesh flaps. We noted any symptoms of SSWS and removed any disintegrated or dead sea stars. To maintain density treatments, we replaced any dead or missing sea stars with similarly sized sea stars collected from the same area and noted their weights and arm lengths. Out of 1165 observations of sea stars in this experiment, we saw 13 instances of wasting symptoms in *Leptasterias* sp. (including 4 deaths) and 11 incidences of wasting symptoms in *P. ochraceus* (including 1 death), or a total of 2.1% cases of SSWS and 0.4% deaths.

Enclosures were removed from the intertidal on 23 and 29 November 2015, and sea stars were brought back to the laboratory. On 24 November and 1 December 2015, wet weights and arm length were remeasured. Due to storm activity, out of 50 original enclosures, 3 enclosures were lost and 10 enclosures had their mesh covers ripped. Since we could not be sure that those sea stars left in ripped enclosures were the same as before the damage, we only analyzed enclosures that were not compromised by ripped covers. Further, to minimize the potential effect on growth of experimental animals, we excluded any enclosures that required replacement of more than one sea star during the experiment. This left us with a total of 27 enclosures, representing between 4 and 6 enclosures per treatment as follows: 6 LL enclosures, 5 PL, 6 MH, 4 LH, and 6 PH.

Our analysis for the competition experiment relied on what could be relatively subtle changes in sea star size over the course of the experiment. Thus, in experimental data sets, we analyzed wet weight data in lieu of data on changes in sea star arm length, as laboratory investigations revealed that sea stars can shrink and extend arms relatively easily and that wet weight is more accurate. In field surveys, however, measuring weight of the 100s of sea stars sampled was unfeasible due to time and scale accuracy limitations, so we analyzed arm length.

2.6. Statistical analyses

All statistical analyses were performed in R version 3.4.3 (R Core Team 2017) with associated packages lme4 (Bates et al. 2015) and lsmeans (Lenth 2016). Our significance level throughout was α = 0.05, but we attempted to interpret results in terms of ecological clarity (Dushoff et al. 2019). To minimize seasonally driven size differences and to provide a reasonable 2014 pre-SSWS baseline, before populations had time to respond to the effects of SSWS (which peaked mid-summer 2014; Menge et al. 2016), we restricted data analyses to spring surveys (April–May) for sea star size, density, and habitat data.

We used linear mixed-effects models to test the prediction that in the field, *Leptasterias* sp. size (arm length in mm) would change after SSWS. Replicate quadrats nested within transect were analyzed as a random effect to account for repeated measures of the same area of intertidal over the course of the 3-yr study and the nested nature of quadrats within transect lines. Although our sites represented a subset of possible study areas, we did not consider site a random effect because we were interested specifically in the effects of site differences (e.g. Menge et al. 2015) on sea star dynamics. We treated year as an ordered

factor. Visual examination of residual plots confirmed that the assumptions of normality and homogeneity of variance were met for final models. As noted above, sampling effort was unbalanced due to sometimes challenging field conditions, so we used a type III sum of squares test to determine the significance of explanatory variables. Use of type III sum of squares tests also facilitated analysis of the important site × year interaction. To calculate final parameter estimates and standard errors for comparison of sea star sizes across sites and years, we refit models using maximum likelihood and conducted post hoc tests using the Bonferroni correction for multiple comparisons (Hothorn et al. 2008). The number of sea stars measured per site/year were as follows — BB: 107 (2014), 126 (2015), 118 (2016); FC: 59 (2014), 765 (2015), 238 (2017); SH: 32 (2014), 307 (2015), 103 (2017); and YB: 95 (2014), 11 (2015), 26 (2017).

To test the prediction that *Leptasterias* sp. density would increase after SSWS, we fit a general linear mixed-effects model with a log(y + 0.1)-transformed response variable, as density data were right-skewed non-normal. Visual examination of residual plots confirmed that assumptions of normality and homogeneity of variance were met for final models. Our model included site, year, the interaction of site and year, *P. ochraceus* density, and a random effect of transect nested within site. We conducted post hoc tests using the Bonferroni correction for multiple comparisons to determine pairwise site differences.

To determine whether *Leptasterias* sp. shifted their distribution vertically between 2014 ('pre'-SSWS) and 2017 (3 yr post-SSWS), we first ordered quadrats by tide height, from the low zone of the intertidal to the high. We then used 2-sample, 2-sided Kolmogorov-Smirnov (K-S) tests with bootstrapped p-values to test the null hypothesis that the vertical distribution of sea stars did not differ among 2014, 2015, and 2017. Because of low *Leptasterias* sp. abundance at Sites SH and YB, we were only able to analyze spatial patterns at Sites BB and FC on Cape Foulweather. Data are presented by absolute tide height to enable the comparison of cumulative distribution across years. Across transects and sites, ecological zones corresponded to slightly different absolute tide heights.

To determine whether *Leptasterias* sp. changed habitat usage (i.e. within versus outside of mussel bed), we conducted a mixed-effects logistic regression model with a logit link function on the binary response of inside or outside of the mussel bed. The fixed effects were site and year, and we included random effects of transect nested in site and replicate

quadrat nested in transect and site. We used ANOVA and Tukey's HSD post hoc tests to determine to what extent experimental density and species identity treatments explained weight change in the competition experiment.

3. RESULTS

3.1. Arm length

We predicted that *Leptasterias* sp. would grow larger in response to SSWS-driven declines in *Pisaster ochraceus* densities. Although *Leptasterias* sp. size did vary among years, it was in the opposite direction from what we predicted: size decreased at all sites over the course of 4 yr post-SSWS onset (Fig. 2, Table S1). The rate of decrease over time varied with site (GLMM site × year interaction F = 5.38, p < 0.001; Fig. 2, Table S1), with the smallest decreases seen at Site BB on Cape Foulweather.

3.2. Density

Also contrary to our prediction, *Leptasterias* sp. density did not vary consistently with year (Fig. 3). However, sea star density differed among sites (Fig. 3) and across years (GLMM site × year interaction, F = 9.29, p < 0.001; Table S2). Additionally, *Leptasterias* sp. density scaled positively with *P. ochraceus* density (GLMM *P. ochraceus* density, F = 21.9, p < 0.001). Out of 1877 total *P. ochraceus* observed in these surveys, 77% (1436) were recruits (arm length < 2.5 cm).
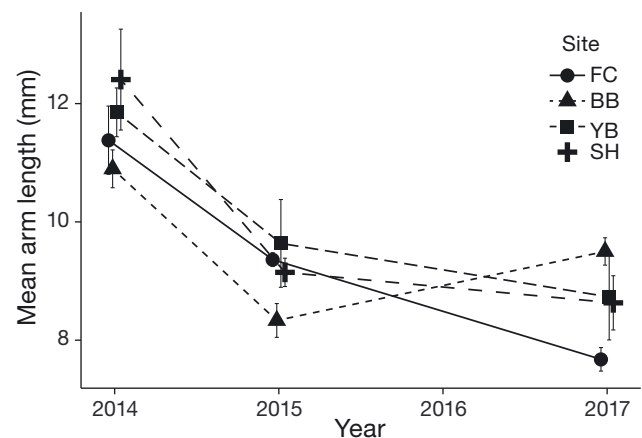

Fig. 2. Mean (±1 SE) *Leptasterias* sp. arm lengths at 4 sites across 4 yr post-sea star wasting syndrome (SSWS; measured in 2014, 2015, and 2017). FC: Fogarty Creek; BB: Boiler Bay; YB: Yachats Beach; SH: Strawberry Hill
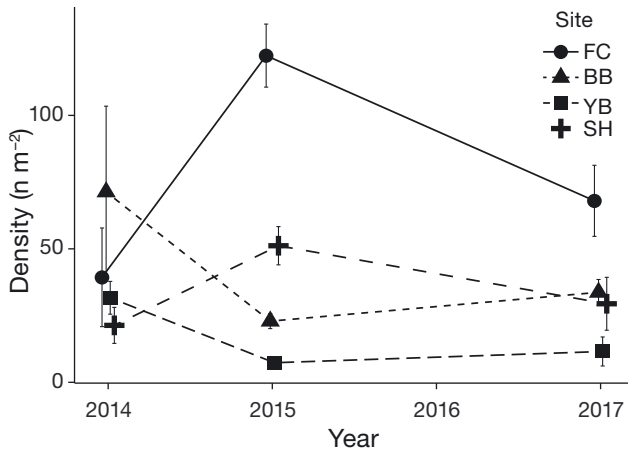
Fig. 3. Mean (±1 SE) *Leptasterias* sp. density at 4 sites across 4 yr post-SSWS (measured in 2014, 2015, and 2017). See Fig. 2 for full site names

3.3. Vertical range and habitat preference

We expected that, in response to SSWS-driven loss of adult *P. ochraceus* biomass, *Leptasterias* sp. would extend their range downward over time. That is, more individuals would be found below, rather than entirely within, the mussel bed. However, vertical spatial patterns of *Leptasterias* sp. at Sites FC and BB did not shift between 2014 and 2017 (2-sample K-S tests; Table S3, Fig. 4). Similarly, the proportion of *Leptasterias* sp. within versus outside of the mussel bed did not change in a clear way from 2014 to 2017 (mixed-effects logistic regression, $\hat{\beta}_{year}$ = 1.074 ± 1.094 SEM, p = 0.425), although the proportion of *Leptasterias* sp. in the mussel bed tended to be higher in 2017 than in 2014 (Fig. 5). Overall, there was on av-

erage a higher proportion of *Leptasterias* sp. in the mussel bed at Site FC (0.73) than at any other site (0.32 at BB, 0.04 at SH, and 0.23 at YB; Fig. 5).

3.4. Competition experiment

As predicted, competition (species identity and density of surrounding sea stars) reduced *P. ochraceus* sea star growth (measured as change in weight from the beginning to the end of the experiment; 1-way ANOVA, $F_{5,27}$ = 8.49, p < 0.0001; Fig. 6). This result was driven by differences between PL and PH treatments (Tukey HSD, p = 0.02), and between recruits in the PL and MH treatments (Tukey HSD, p = 0.06). However, growth of *P. ochraceus* in the MH treatment did not differ from that in PH treatments (Tukey HSD, p = 0.997). *Leptasterias* sp. growth was unaffected by treatment, and all *Leptasterias* sp. lost weight over the course of the experiment. Both sea star species consumed mussel prey during the experiment: on average, the proportion of mussels eaten between each monthly sampling was (mean ± SE for each treatment) 0.60 ± 0.06 for LL, 0.86 ± 0.04 for LH, 0.85 ± 0.05 for MH, 0.77 ± 0.06 for PL, and 0.78 ± 0.06 for PH.

4. DISCUSSION

Following mass mortality of the keystone predator *Pisaster ochraceus* from SSWS, ecological release theory predicts that populations of subordinate predators may increase as pressure from competition and/or predation is reduced. Our study pursued multiple lines
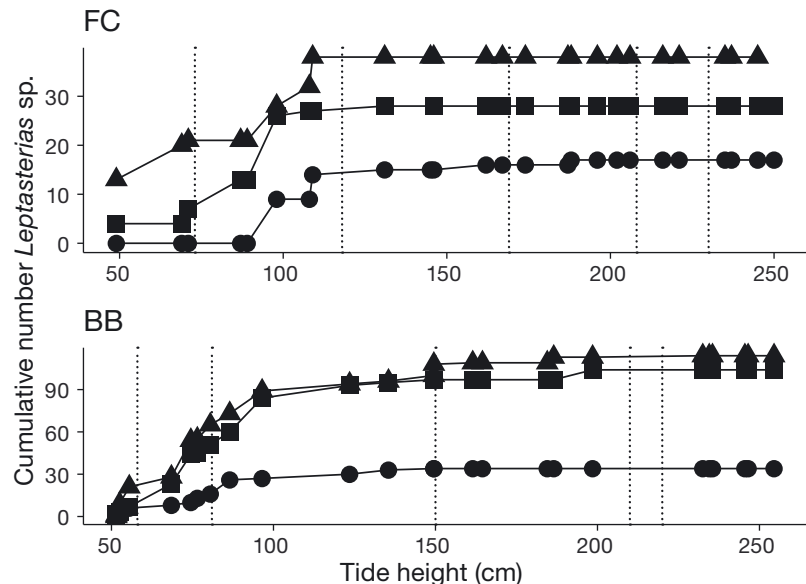

Fig. 4. Cumulative distributions of *Leptasterias* sp. observations by tide height for 2014 (immediately post-SSWS, circles), 2015 (triangles), and 2017 (squares, 4 yr after SSWS onset). Ecological zones represented include (listed from low to high): low intertidal zone upper edge (dominated by algae and barnacles), mussel bed lower edge, mussel bed middle, mussel bed upper edge, and high zone. Average tidal height at each successive ecological zone is represented by dotted vertical lines. FC: Fogarty Creek; BB: Boiler Bay
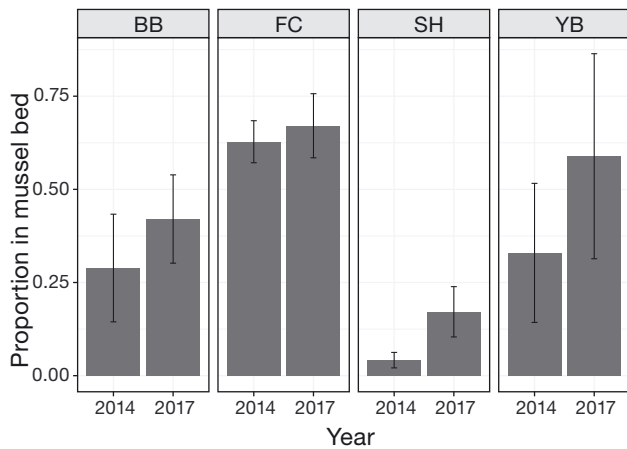
Fig. 5. Mean (±1 SE) proportion of observed *Leptasterias* sp. in mussel bed, relative to just below it, at 4 sites in 2014 and 2017. See Fig. 2 for full site names
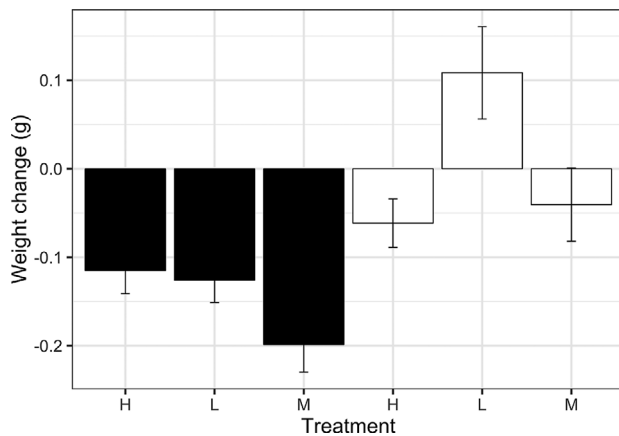

Fig. 6. Mean (±1 SE) weight change over the course of the 3 mo experiment for *Leptasterias* sp. (black bars) and *Pisaster ochraceus* (white bars) across competition treatments. Treatments were: H = 8 conspecifics (high density); L = 4 conspecifics (low density); M = mixed (4 of each species). Sample sizes (number of enclosures) for each treatment were: *Leptasterias* sp. L = 6; *P. ochraceus* L = 5; M = 6; *Leptasterias* sp. H = 4; and *P. ochraceus* H = 6

of inquiry to test whether the population dynamics of *Leptasterias* sp. sea stars follow expectations of ecological release, and whether they may thereby influence *P. ochraceus* recovery. Contrary to expectation, *Leptasterias* sp. appear unlikely to modulate *P. ochraceus* population recovery from SSWS. These 2 sea star species do not appear to be in direct competition in Oregon, as they were in the San Juan Islands, WA, USA (Menge 1972a,b, 1975). Further, *Leptasterias* sp. population dynamics did not respond to reduced *P. ochraceus* abundance as expected from ecological release theory at any of our sites. In fact, at all sites, *Leptasterias* sp. population size distributions shifted towards smaller individuals in the wake of SSWS.

Our observations are consistent with the results of another study of the response of subordinate predators to SSWS in Oregon (Cerny-Chipman et al. 2017), which investigated population response of 2 species of whelks, small predatory intertidal snails, to the SSWS outbreak. At the same study sites as used here, Cerny-Chipman et al. (2017) found that whelk size distributions shifted toward smaller individuals in the year following SSWS, a result they attributed to increased success of recruitment. However, unlike Cerny-Chipman et al. (2017), we found no evidence for coincident *Leptasterias* sp. density increases at any sites except FC, a site with historically high abundances of *Leptasterias* sp. and relatively lower prey productivity (Menge et al. 2015). The lack of density increase suggests that increased reproductive success may not account for the size distribution change. However, because finding very small (i.e. 2–3 mm diameter) *Leptasterias* sp. within a mussel bed matrix can be challenging, it is likely that some were missed by our non-destructive sampling approach. If recruitment did increase but some small stars were missed, this would explain the observed trends of decreasing size coupled with stable densities. Alternatively, the shift towards smaller *Leptasterias* sp. seen here may be attributable to a change in reproductive timing, i.e. delayed reproduction leading to smaller recruits at the time of the surveys. It also may reflect lower or negative growth rates, such as those observed in the field experiment, due (for example) to increased environmental stress or sublethal effects of SSWS. These changes may be related to an environmental change, as the 'natural experiment' aspect of SSWS precludes controlling environmental conditions. For example, coincidentally with SSWS, a marine warming event occurred in 2015 and 2016 (Barth et al. 2018), leading to warmer than usual temperatures at coastal sites (B. A. Menge unpubl. data). Deeper understanding of the processes that determine *Leptasterias* sp. reproductive dynamics and growth rates could help determine the relative likelihood of these alternative explanations.

Unlike in the San Juan Islands, where studies showed that *P. ochraceus* and *Leptasterias* sp. were in direct competition for food (Menge 1972a,b, 1975, Menge & Menge 1974), we did not find evidence for competition between *P. ochraceus* recruits and adult *Leptasterias* sp. in our field experiment. That is, *P. ochraceus* recruit growth was unaffected by *Leptasterias* sp. presence. In fact, sea star density was more important than species identity, where additional sea stars of either species limited the growth of *P. ochraceus* recruits. Similarly, *P. ochraceus* presence and

density did not affect *Leptasterias* sp. growth. Survey results showing that *Leptasterias* sp. did not generally become larger, more abundant, or change their habitat use in response to the lowered abundance of adult *P. ochraceus* strengthen this conclusion. In addition, the abundances of *P. ochraceus* and *Leptasterias* sp. were positively related in our surveys. We conclude that in Oregon, unlike in the San Juan Islands, these sea stars did not compete for food. The lack of competition between *Leptasterias* sp. and *P. ochraceus* removes the mechanisms behind our main predictions that (1) *Leptasterias* sp. populations would change in ways consistent with ecological release after disease-driven loss of *P. ochraceus*, and (2) interactions with *Leptasterias* sp. would provide a bottleneck to *P. ochraceus* population recovery. In the absence of strong competitive interactions between *Leptasterias* sp. and *P. ochraceus*, these predictions do not hold.

4.1. Potential explanations

Given the previous results in the San Juan Islands, why did these species not compete at our Oregon sites? We see several possible explanations. For example, the *Leptasterias* sp. species studied in Washington may have differed from that in Oregon. The genus *Leptasterias* in the Pacific Northwest represents a species complex that may include *L. hexactis*, *L. pusilla*, *L. epichlora*, and *L. aequalis*, the latter of which is thought to be a hybrid of *L. hexactis* and *L. epichlora* (Kozloff 1996). These species are difficult to distinguish visually and their taxonomy has not yet been fully resolved. Thus, ecological differences between species are not well understood and may account for differences in the *Leptasterias* sp.–*P. ochraceus* interaction observed in this study versus earlier work.

However, we believe it is more likely that important differences in the intertidal habitat in the San Juan Islands versus the Oregon coast are responsible for the observed results. First, wave energy differs greatly between the 2 regions, with much higher wave energy on the open Oregon coast than in the San Juan Islands. The size of *Leptasterias* sp. in the Oregon intertidal zone may be more limited by the risk of dislodgement from waves limiting foraging activity than by interspecific competition with *P. ochraceus* for resources. Second, Oregon *Leptasterias* sp. occur most abundantly within the *Mytilus californianus* matrix (i.e. on the mussels and in the byssal 'forest' beneath the mussels), while *P. ochra-*

ceus adults occur in the low zone and forage mostly at the lower edge of the mussel bed. The mussel matrix habitat is generally absent in the San Juan Islands, where *M. californianus* are largely replaced by large barnacles and fucoid algae (e.g. Dayton 1971). There, *Leptasterias* sp., by necessity, co-occur with *P. ochraceus* on the lower shore, and both use crevices, channels, and boulder undersides as their primary habitat and thus, when abundant, likely experience frequent interspecific contact (Menge 1972b). Third, although *P. ochraceus* juveniles were abundant during the few years of this study, historically, *P. ochraceus* recruitment is low (both in the San Juan Islands and on the Oregon coast; Menge & Menge 1974, Menge et al. 2016). Thus, contact between similar-sized animals of each species (i.e. adult *Leptasterias* sp. and *P. ochraceus* recruits) likely has been temporally sporadic at best, suggesting little selective pressure for competition-related adaptation. Fourth, benthic invertebrate prey availability is much higher on the Oregon's open coast relative to the San Juan Islands, which may preclude food competition. Prey (barnacles, mussels, limpets, chitons, snails) recruitment has been measured as 2.8 times lower on average in the San Juan Islands than in Oregon (B. A. Menge unpubl. data). In the San Juan Islands as compared to the Oregon coast, relatively lower prey recruitment may create conditions of food limitation, thus driving interspecific competition. A higher rate of prey input in Oregon than in the San Juan Islands may mean that food resources are not limiting for juvenile *P. ochraceus*, despite having a diet similar to that of *Leptasterias* sp., leading to little or no interspecific competition.

We believe that the combination of food resource supply and habitat overlap drives the observed differences between this study and the earlier work in the San Juan Islands. Our hypothesized mechanisms are summarized conceptually in Fig. 7. In Oregon, where resource supply is high and habitat overlap is low, competition with *P. ochraceus* is not a driving factor for *Leptasterias* sp. abundance and size structure. Therefore, we did not see competitive release after SSWS. In contrast, in the San Juan Islands, where food supply is low and likely more limiting, and habitat overlap is high, we may have seen competitive release after SSWS-related loss of *P. ochraceus*. Indeed, this hypothesis is supported by recent research surveying sea star populations in the sheltered Burrard Inlet, BC, Canada, near the San Juan Islands, which documented an increase in abundance of the sea star *Evasterias troschelii* following *P. ochraceus* loss from SSWS (Kay et al. 2019).
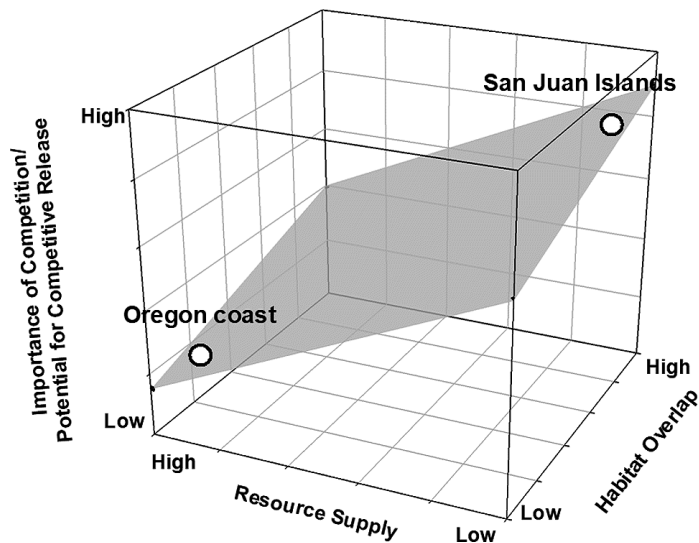
Fig. 7. Conceptual diagram of proposed mechanisms driving difference in sea star competition between the San Juan Islands and the Oregon coast. In the San Juan Islands (represented by the area in the upper right of diagram), habitat overlap is high, resource supply is low, and there is a high potential for competitive release in *Leptasterias* sp. due to a high importance of competition between *Leptasterias* sp. and *Pisaster ochraceus*. In contrast, on the Oregon coast, habitat overlap is low, resource supply is high, and competition with *P. ochraceus* is not a driving factor for *Leptasterias* sp. population dynamics. Therefore, the potential for competitive release in *Leptasterias* sp. following SSWS-driven declines of *P. ochraceus* is low

4.2. Implications for community dynamics in the Oregon intertidal

Our results were remarkably consistent across sites representing a range of prey productivity and predator population dynamics. In general, Cape Perpetua sites (YB and SH) are characterized by relatively high mussel and barnacle productivity, high densities of *P. ochraceus* (pre-SSWS), and low abundances of *Leptasterias* sp. relative to Cape Foulweather (FC and BB) sites (Menge et al. 2015). Despite these differences, *Leptasterias* sp. size decreased at all sites post-SSWS. However, site-specific differences did emerge. *Leptasterias* sp. densities were higher post-SSWS at FC, a finding that may be attributable to the historically high density of *Leptasterias* sp. at that site. In addition, there was a consistently higher proportion of *Leptasterias* sp. in the mussel bed at FC than at any other site, likely due to limitations of prey below the mussels as a result of preemption by high algal cover and high availability of epibiotic prey (small barnacles and limpets) on mussel shells (J. Sullivan-Stack and B. A. Menge pers. obs.).

4.3. Conclusions

In summary, we found that *Leptasterias* sp. populations are unlikely to provide a bottleneck for *P. ochraceus* recovery from SSWS, and that their dynamics did not respond strongly to SSWS in the 4 yr immediately following catastrophic adult *P. ochraceus* loss. Our predictions were based on ecological theory and previous research on these sea stars in the northeast Pacific. However, important differences across the 2 regions studied, namely in habitat overlap and resource availability, may have driven strong interspecific resource competition in one area (the San Juan Islands) but not another (the Oregon coast). Thus, this research emphasizes that we must take into account specific contexts, particularly with respect to resource supply and habitat, when attempting to predict the occurrence and consequences of ecological release. This research provides a cautionary tale for anticipating and managing outbreaks that result from ecological release, which are often of strong concern for conservation.

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